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Trait changes in a harvested population are driven by a dynamic tug-of-war between natural and harvest selection

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1 Selective harvest of large individuals should alter natural adaptive landscapes and
2 drive evolution towards reduced somatic growth and increased reproductive
3 investment. However, few studies have simultaneously considered the relative
4 importance of artificial and natural selections in driving trait changes in wild
5 populations. Using 50 years of individual-based data on Windermere pike (*Esox*
6 *lucius*), we show that trait changes tracked the adaptive peak, which moved in the
7 direction imposed by the dominating selective force. Individual lifetime somatic
8 growth decreased at the start of the time series because harvest selection was
9 strong and natural selection was too weak to override the strength of harvest
10 selection. However, natural selection favoring fast somatic growth strengthened
11 across the time series in parallel with the increase in pike abundance and,
12 presumably, cannibalism. Harvest selection was overridden by natural selection
13 when the fishing effort dwindled, triggering a rapid increase in pike somatic
14 growth. The two selective forces appear to have acted in concert during only one
15 short period of prey collapse that favored slow-growing pike. Moreover, increased
16 somatic growth occurred concurrently with a reduction in reproductive investment
17 in young and small female pike, indicating a trade-off between growth and
18 reproduction. The age-specific amplitude of this change paralleled the age-specific
19 strength of harvest pressure, suggesting that reduced investment was also a
20 response to increased life expectancy. This is the first study to demonstrate that a
21 consideration of both natural selection and artificial selection is needed to fully
22 explain time-varying trait dynamics in harvested populations.

Selective harvest of the largest individuals may add a strong and temporally consistent directional component to the natural selective forces shaping adaptive landscapes (1). Theory predicts that such consistent selection should induce life history evolution (2-4). Accordingly, recent studies in nature indicate a correlation between increased harvest pressure and phenotypic changes in plants (5) and vertebrates (6). Harvest-induced phenotypic changes have been studied extensively in fisheries, where harvest is often associated with decreased somatic growth and/or decreased age and size at maturity (7-9). Under laboratory conditions, artificial selection against large size has been shown to induce rapid evolution towards slower growth (10), and to promote genetically-based reductions in fecundity, larval viability, and foraging efficiency (11). These harvest-induced changes are generally considered maladaptive (11), because harvest and natural selection can act in different directions (1). However, to date, no study has examined the relative contributions of harvest and natural selection in driving trait changes in wild, harvested populations. We performed this task in pike (*Esox lucius*) from Windermere (UK). This system is particularly well-suited for this endeavor because we have previously demonstrated that natural and fishery selection act in opposite directions on Windermere pike body size (1).

Windermere is a glacial valley lake divided by shallows into two basins of different productivity and constituting different habitats for pike (12, 13) (Fig. 1A). Commercial net fisheries for several species including pike have operated on Windermere since the 12th century but were terminated in 1921 due to heavy fishing problems (13). Le Cren (13) suggested that, by 1939, the fish population of Windermere consisted mainly of a dense population of perch (*Perca fluviatilis*) and a moderate population of pike feeding mostly on perch and, to a lesser degree, charr (*Salvelinus alpinus*) and trout (*Salmo trutta*). Gillnet fishing for pike was initiated in 1944 with two

objectives: (i) increase the density of perch (by far the most abundant prey item in pike diets (14)), which were used as human food during wartime and (ii) to provide information that would illuminate the overfishing problem (13). The fishing methods for pike and gear used (64 mm mesh size gill-nets) remained constant until the present time, but the exploitation rate decreased overall to reach a very low level after 1980 (Fig. 1C). The scientific fishery is the only removal fishery for pike and targets individuals longer than 55 cm (15), although recent evidence suggests that the largest pike are less susceptible to capture (1). Male and female pike typically mature at age 2 (i.e., before recruitment to the fishery which occurs mainly at age 3 for females and 4 for males (15)). Captured pike are measured for body length (cm, measured as fork length), weighed (kg), sexed, and opercular bones are removed for age and length back-calculation following a method validated for Windermere pike by Frost and Kipling (16). Bone density differs between summer and winter, producing narrow bands (hereafter “check”) that are deposited on the opercular bones during slow winter growth. These checks then serve as an annual mark and, thus, allow the aging of individual fish. An individual’s length is back-calculated at each age using a relationship between the radius of the opercular bone at each check and body length (16). In the present work, the growth data therefore represent length-at-age data collected on individual pike from age-1 to age-at-capture. In addition to growth data, data on female reproductive investment (gonad-weight, egg-number and egg-weight, which is a proxy for egg-size) were collected since 1963 (15), which coincides with the time that the exploitation rate dropped (Fig. 1C). Together with these biological data, surface water temperatures were recorded on a near daily basis and were here averaged for each year. Finally, the abundance of pike and perch have been estimated annually

for the 1944-1995 period, separately for each basin as well as separately for young (age = 2) and old individuals (age > 2) (17).

Natural and harvest selection have been previously quantified for the Windermere pike population through an estimation of the strength, direction, and form (directional, nonlinear) of the two selective forces (1). This earlier work demonstrated that harvest and natural selection often acted in opposite directions on pike body length (1). In particular, directional natural selection tended to favor long pike whereas the fishery targeted long individuals. Moreover, nonlinear natural selection tended to be stabilizing in Windermere, favoring pike of intermediate lengths, whereas fishery selection tended to be disruptive, favoring short and long pike (1). Large pike presumably have an advantage over small pike in terms of natural selection in that they are not susceptible to cannibalism, which can be severe in pike (18). Moreover, large pike likely have an advantage in terms of intrasexual combat for females during the breeding season (18).

The context for selection in Windermere changed across the five decades of study. From 1944 to 1995, pike numbers increased while perch numbers declined over the same period (Fig. 1B), likely resulting in increased agonistic interactions and cannibalism within the pike population. Consistent with this view, selection analyses indicate that stabilizing selection acting on Windermere pike body length overall strengthened through time (1) (i.e., that natural selection favoring fast somatic growth to reach the optimum length has increased). However, natural selection often fluctuates in connection with severe environmental variations (19). In Windermere, collapse of the perch population due to a disease outbreak in 1976 (20) was likely the most severe environmental disturbance experienced by pike across the entire time series (Fig. 1B). Severe food stresses have been shown to select against fast growth (21). Therefore,

ignoring fishery selection, we hypothesized that natural selection would drive an increase in pike somatic growth across the study period, except when the perch population collapsed in 1976. However, we also expected the fishery to simultaneously operate in the opposite direction and consistently drive decreased growth, but with a lesser effect when fishing intensity was reduced. Finally, if natural selection drove evolutionary change towards faster somatic growth, we would also expect a concurrent reduction in reproductive investment due to the trade-off between growth and reproduction (2, 3).

To test these hypotheses in a robust framework, we used mixed-effects models ((22), see also Materials and methods for an extensive description of our models). In these models we have taken into account the many possible environmental variables (i.e., basin productivity, water temperature, pike numbers, and prey density) known to plastically affect somatic growth (e.g., increased abundance may reduce growth through a density-dependent food limitation). Additionally, because reproductive decisions are also functions of surplus energy gained prior to spawning (23), we have taken into account the effect of somatic body condition (hereafter "fatness") in estimating changes in individual reproductive investment (see Materials and methods). By considering the potential effects of harvest selection and natural selection, we demonstrate that both selective forces played a role in driving trait changes in Windermere pike across five decades.

Results

We first tested for an overall change in pike somatic growth across the entire time series by modeling the linear effect of time on individual lifetime growth (asymptotic length, see Materials and methods). We found that pike somatic growth increased significantly

over the 1944-1995 period (Table 1). To evaluate shorter time-scale changes in relation to periods of varying strengths of natural and fishery selection, we modeled nonlinear changes in individual pike lifetime growth (Fig. 1D, see Materials and methods). The nonlinear trend, shown in Fig. 1D, may be separated into 4 phases, which we describe below.

During the first phase, from 1944 to the early 1960's, somatic growth slightly decreased, suggesting that the selection imposed by fishing overwhelmed the strength of natural selection. There was a remarkably close match between the peak of fishing pressure in 1963 (Fig. 1C) and the slowest growth observed across the entire time series in year classes born from 1960 to 1963 (Fig. 1D) (i.e., year classes for which both the parents and the offspring experienced strong fishing pressure). During the second phase, 1963 to the mid-1970's, pike somatic growth increased rapidly, suggesting that natural selection overwhelmed fishery selection during this time period (Fig. 1D). Pike somatic growth stabilized in fish born in the early 1970's, suggesting that phenotypic adjustment to the new adaptive peak took approximately 10 years, a delay corresponding to 2 to 5 pike generations (i.e., Windermere pike first reproduce at age 2 but the mean generation time, calculated as the mean age of mature females weighed by their gonad weight, was estimated to be 5.2 years). During the third phase, from the mid-1970's through the mid-1980's, pike somatic growth decreased slightly, most likely due to an inversion in the direction of natural selection that then acted in concert with fishery selection. Indeed, in 1976 a disease outbreak induced a collapse of the perch population (20) while pike numbers were relatively high (Fig. 1B). Food stress might have thus induced starvation that ultimately selected against fast growth (21). The perch collapse was followed by a sharp decrease in pike numbers (Fig. 1B), supporting the view that prey shortage induced selection in the pike population through severe starvation. During the fourth

phase, from the mid-1980's to the mid-1990's, pike somatic growth increased very rapidly, a period corresponding to the highest pike numbers of the time series, the lowest fishing pressure, and relatively low and fluctuating perch densities (Figs. 1B and 1C).

Overall, this nonlinear trend confirms that fishery and natural selection were operating simultaneously in opposite directions (1) and also supports the prediction that pike somatic growth variation responded to the dominant selective force. Fishery selection was overwhelmed by natural selection during the early 1960's (leading to the change from phase 1 to phase 2). Additionally, females grew faster than males overall, and increased their growth rates at a faster rate than males over the study period (Table 1). This later result indicates that, as faster growers, females experienced stronger fishery selection than males, and thus benefited more from the relaxation in the fishing pressure later in the time series. Finally, pike grew significantly faster in the more productive south basin compared to the less productive north basin (Table 1).

Concurrent with the increase in somatic growth after the early 1960's, we found that young – but not old – female pike reduced their reproductive investment (Fig. 2, Table 1), providing support for our third hypothesis of a trade-off between growth and reproduction in Windermere pike. Indeed, the age-specific intercept of the reproductive investment/length reaction norm decreased significantly for gonad-weight and egg-number, but not egg-weight (Fig. 2, *Year* effect in Table 1). Egg-weight is positively correlated to offspring size, and competition is predicted to favor large egg-size (3). Hence, maintenance of egg-weight despite decreased investment suggests increased competition in young pike in connection with increased pike density. At the same time, the age-specific slope of the investment/length reaction norm increased, indicating that female pike were investing in reproduction at a larger size (Fig. 2). This increase in the

*Length*Year* interaction was statistically significant for gonad-weight and egg-number but not egg-weight (Table 1). In contrast, at any given length, the age at which investment occurred (*Age*Year* interaction) increased significantly for egg-weight only (Table 1). Finally, the magnitude of the aforementioned changes in investment decreased significantly with the age for both gonad-weight and egg-weight (Fig. 2, *Length*Year*Age* interaction in Table 1). In order to determine whether this *Length*Year*Age* effect was related to age-specific differences in the relaxation of fishery selection after the early 1960's, we calculated age-specific mean fishery selection differentials for females at each age (see Materials and methods). We found that fishery selection decreased with increasing age, and was substantial on age 3 females only (Fig. 2), supporting the view that reduced reproductive investment was not only a response to strengthening natural selection but also related to increased life expectancy. Finally, somatic body condition had a positive effect on investment (significant on gonad-weight and egg-number, Table 1), confirming that surplus energy gained prior to reproduction plastically affects energy allocation to reproduction (23).

Discussion

Wild populations are continually subject to natural selection, which temporally fluctuates in direction and/or magnitude (19). Natural selection acting on Windermere pike is presumably a function of both conspecific and prey (perch) densities. Prior to 1944, pike abundance was relatively low while perch were abundant (13), presumably creating conditions for weak competition for food and low cannibalism (i.e., weak natural selection for fast growth). However, throughout most of the time series under consideration, pike abundance was increasing while perch abundance was decreasing. These conditions set the stage for selection favoring fast growth presumably through

cannibalism, because encounter rates between pike were increasing while prey abundance remained high enough to support fast growth in pike. However, the perch collapse in the mid-1970's seemed to reverse this trend during a short period by selecting for slow growth. This result provides support for previous work which suggested that nutrient stress is a strong agent of selection against fast somatic growth in both plants and animals (21). Together, these results suggest that the fitness of fast growing pike as a function of the pike/perch ratio is dome-shaped in Windermere (i.e., for a pike, relatively large size confers fitness advantages as long as prey abundance is not too low). Cannibalism is generally considered as a "life-boat" mechanism allowing populations to survive under decreased food conditions (24). Our results lead us to modify this point of view by also suggesting that cannibalism can result in growth costs, which may be detrimental under very severe food stress.

The fishery for pike in Windermere consistently selected against fast growth, but the strength of this artificial selective force decreased across the time series. From the early 1940's to the early 1960's (phase 1), fishery selection was strong enough to override natural selection. The result was that combined selection favored decreased somatic growth during this time period. During phase 2 (~10 years), relaxed fishing pressure allowed natural selection to prevail and resulted in combined selection favoring increased somatic growth. Phenotypic adjustment to the new adaptive optimum was remarkably fast (2 to 5 generations). This result suggests that two slightly different evolutionary processes were at work. Average heritability for growth in fish ($h^2=0.3$) is high enough to cause substantial evolution in a few generations (25). However, due to the very detailed data used here we probably also observed direct effects of the fishery (i.e., direct removal of fast growing genotypes). Indeed, the slowest growth occurred in year classes that immediately preceded the peak of fishing pressure (i.e., in year classes

that were born from parents that were strongly fished and that were themselves strongly fished). Consequently, relaxed fishing pressure immediately increased the proportion of fast growing genotypes in the population. Interestingly, Carlson et al. (1) did not observe any significant change in the strength of directional selection acting on Windermere pike (i.e., selection pushing the population towards the newly emerging adaptive peak). They suggested that this was possibly due to the fact that pike quickly attained equilibrium after fishing effort dwindled (1). Our results provide support for their assertion.

We show that a rapid shift towards fast growth following decreased fishing pressure was accompanied by a reduction in reproductive investment in young and small females. This result strongly supports the prediction of a genetic trade-off between growth and reproduction in Windermere pike (2, 3). Importantly, we have accounted for the plastic effect of short-term variations in growth conditions in our reaction norm approach. Indeed, in teleosts plasticity in reproductive decisions is affected by the rate of surplus energy gained during critical periods (23). In Windermere pike, energy used for reproduction in March and April is gained during the previous summer (15). We have here estimated surplus energy gained during previous summer as the somatic body condition (fatness) at capture, and we show that condition had a positive effect on investment. After accounting for this plastic effect, we found that investment at each reproduction decreased while the length at which investment occurred increased. We further show that the age-specific amplitude of this later change paralleled with the age-specific strength of fishing selection, suggesting that investment change was partly a response to relaxation in the fishing pressure. Hence, our results provide further support for previous research, which suggested that fisheries may induce genetic change in the energy allocation rules to growth and reproduction in fish

populations (2, 4). Instead of investing in gonads early in life and at a small size due to fishery-induced mortality, Windermere female pike now grow first to increase fitness through the achievement of a larger size.

Our data suggest that up-to-1963 exploitation rates of 1.1 to 7.3 % (mean = 3.3 %) were enough to impede the effects of natural selection in Windermere pike and even cause detectable evolution in the opposite direction. It is thus highly probable that commercial harvest, that may deplete 45 to 99 % of the reproductive biomass (26), may cause rapid evolution in commercial fish stocks. Temporal consistency of harvest practices (e.g., systematic removal of the largest individuals) likely magnifies the evolutionary impacts of exploitation. Introducing variety in harvest practices could limit the amplitude of harvest-induced trait changes. However, our results point out that knowing the intensity and direction of artificial selection is not always enough to predict the response of populations to harvest. Instead, trait changes result from the combined forces of both the harvest and natural selection, and evolution of harvested populations is thus a process more complex than generally portrayed. Conservation plans that ignore this complexity could lead to improper management decisions.

Materials and methods

Growth modeling

We have tested for linear change in growth during the 1944-1995 period using a nonlinear mixed-effects model (random grouping factor $n = 13,942$ individuals, $n = 65,123$ observations). This model was based on the von Bertalanffy growth curve (hereafter "VBGC", fitted to length-at-age data for each individual) and allowed us to quantify the temporal trend in individual asymptotic length. Asymptotic length is an index of lifetime somatic growth rate. The index thus synthesizes an individual's

decisions for energy allocation, and is particularly powerful to study life-history variation and evolution. The trend in asymptotic length was estimated while simultaneously controlling for the effect of basin productivity, and the effects of yearly variations in water temperature, prey numbers, and pike density. Individual pike growth was modeled with a 3 parameter formulation of the VBGC (27): $L(A)=\alpha+(\beta-\alpha)\gamma^A$, where L =length (in cm), A =age, β =intercept, γ =rate of increase, and α =asymptotic length. This formulation of the VBGC yielded the lowest Akaike's Information Criterion (AIC) and less structure in the residuals compared with 6 other formulations of the VBGC and 8 other nonlinear models (the Gompertz, 3 and 4 parameters logistic, Pauly's, Morgan, Mercer and Flodin, Weibul, modified Freundlich, Chapman-Richards, and Michaelis-Menten models (27)). The selected VBGC equation was incorporated into a restricted maximum likelihood (REML) nonlinear mixed-effects model (22) (nlme library of R (28)):

$$L_{ij}=\alpha_{ij}+(\beta-\alpha_{ij})\gamma^{A_{ij}}+\epsilon_{ij} \quad (\text{Eq. 1})$$

where L_{ij} is length of individual i in year j , ϵ_{ij} is a normally distributed within-individual error term and the parameter α_{ij} is associated with fixed covariate effects and a random individual effect:

$$\alpha_{ij}=\beta_0+\beta_1 T_j+\beta_2 Y_{pij}+\beta_3 O_{pij}+\beta_4 Y_{pej}+\beta_5 O_{pej}+\beta_6 Bas_i+\beta_7 S_i+\beta_8 Y_i+\beta_9 T_j*Y_{pij}+\beta_{10} T_j*O_{pij}+\beta_{11} T_j*Y_{pej}+\beta_{12} T_j*O_{pej}+\beta_{13} Y_j*S_i+b_i \quad (\text{Eq. 2})$$

where β_s =model coefficients for the fixed-effects part where Y =Year, S =Sex, Bas =Basin, T =Temperature, Y_{pi} =Young pike (age=2), O_{pi} =Old pike (age>2),

Y_{pe} =Young perch ($age=2$), O_{pe} =Old perch ($age>2$), and b_i is a normally distributed random individual effect. Interaction between temperature and each biological covariate accounted for the thermal dependence of food conversion efficiency and predator-prey overlap, and generated very significant improvement of model AIC compared to a simple additive formulation. Estimate of the main effects of Y and S (Table 1) was obtained from a model in which the $Y*S$ interaction was omitted from (Eq. 2). Both models incorporated within-individual temporal autocorrelation (autoregressive function of time of order 1) and handled heteroscedasticity by modeling the variance of ε_{ij} as the product of a sex-specific power function of A and a linear function of Y . Fig. 1D was obtained from a generalized additive mixed effects model (GAMM, mgcv library of R (29)) in which individual asymptotic length (α_i) was the response [computed from a model similar to (Eq. 1, Eq. 2) above, except that the fixed effects part did not contain any covariate ($\alpha_i=\beta_0+b_i$ in (Eq. 2)], grouped by S , nested in Bas , nested in $year\ class$ (random grouping factor $n = 197$ groups, $n = 13,942$ individuals). In the GAMM, predictors were as in (Eq.2) with no $Y*S$ interaction, covariates were averaged across individual life, and the linear Y effect was replaced by a nonlinear $year\ class$ effect (natural quadratic spline), thus removing any *a priori* expectation concerning the shape of the trend.

Reproductive investment modeling

We have tested for temporal changes in the slope and intercept of the reproductive investment/body length reaction norm of females born from 1963 to 1995 using linear mixed-effects models including the full interaction between length, age, and time as continuous variables (random grouping factor $n = 41$ years, $n = 3,070$ observations).

Rep_{ij} represents gonad-weight, egg-number (both ln-transformed), or egg-weight of individual *i* in year *j*, and were modeled with REML linear mixed-effects models:

$$\text{Rep}_{ij} = \beta_0 + \beta_1 A_{ij} + (\beta_2 + b_{1j}) \ln L_{ij} + \beta_3 Y_j + \beta_4 M_i + \beta_5 \text{Kns}_i + \beta_6 \ln L_{ij} * Y_j + \beta_7 A_{ij} * \ln L_{ij} + \beta_8 Y_j * A_{ij} + \beta_9 A_{ij} * \ln L_{ij} * Y_j + b_{2j} + \varepsilon_{ij} \quad (\text{Eq. 3})$$

where β s=model coefficients for the fixed-effects part, b_{1j} and b_{2j} are normally distributed random year-effects (with a symmetric covariance matrix), and ε_{ij} is a normally distributed within-year error. Fixed-effect covariates were A =age, $\ln L$ =natural log of length (in cm), Y =year (continuous variable), M =month of capture (from October to February). Kns was the relative somatic condition factor (30): $\text{Kns} = 100 * \text{SM} / \text{SM}_{\text{std}}$, where SM is the somatic mass (total mass-gonad mass) and SM_{std} is the predicted somatic mass of a fish of the same length L , as calculated from the $\ln(\text{SM}) - \ln(L)$ regression equation (least squares mean fit, $N=3,694$; $R^2=0.96$). Somatic body condition was found to have a higher effect on reproductive investment than previous growth history (α and last growth increment) during model selection procedure based on AIC. The M effect on egg-number was not significant and was thus omitted from egg-number modeling. Estimates of the main effects of $\ln L$, A and Y (Table 1), were obtained from a model in which the interactions were omitted from (Eq. 3). The models handled heteroscedasticity by modeling the variance of ε_{ij} as the product of exponential functions of A and $\ln L$. Predicted values in Fig. 2 were computed from the interaction model. Finally, selection differentials provided in the reproductive investment analysis and in Fig. 2 were estimated for each year and each age as the mean backcalculated length of females that escaped the fishery (but were caught eventually) minus the mean

length of females of the same age caught into the fishery (9) for the entire study period (1945-1995).

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Author contributions. E.E. and S.M.C. conceived the study. E.E. and L.C.S. performed the statistical analyses. E.E. wrote the paper in dialogue with all coauthors, all of whom participated in the interpretation of the statistical results. I.J.W., J.M.F. and J.B.J. contributed to the collection of data and made them all available to the present study, and T.O.H. organized the data set.

Author information. The authors declare that they have no conflicts of interests. Correspondence and requests for materials should be addressed to N.C.S. (n.c.stenseth@bio.uio.no).

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Figure legends

Fig. 1. Windermere background information and growth time series for pike (*Esox lucius*). **(A)** Map showing the location of the study lake (surface area 14.8 km²) in the Lake District of north-west England, U.K., and the division of the lake into two basins. The southern basin is morphologically different from and more productive than the northern basin. **(B)** Population size of pike (purple) and perch (bold, blue) showing increased numbers of the predator and decreased numbers of the main prey (log 10 scale). Dashed lines represent age 2 individuals (termed “young”), solid lines represent age 3 and older individuals (termed “old”). **(C)** Exploitation rate for pike with trendline, representing the proportion of pike caught in the fishery during the winter compared to the number of pike in the lake the previous spring. **(D)** Nonlinear temporal trend in individual pike growth with 95% confidence intervals taking into account the effects of variations in growth conditions (see Materials and methods). Points represent the partial residuals for the smooth term (i.e., the residuals that would be obtained by dropping the term concerned from the model while leaving all other estimates fixed).

Fig. 2. Changes in the gonad weight/body length reaction norm of age-3 to age-8 female pike in Windermere. Lines represent predicted values for 1963 (bold, red) and 2003 (blue) with 95% confidence intervals (dotted lines), and were estimated from data for the 1963 to 1995 year classes. S is the age-specific mean selection differential (in cm, \pm SD) from fishery selection on females from 1945 to 1995 (see Materials and methods). Decrease in the intercept of the investment/body length reaction norm (*Year* effect in Table 1) indicates decreased investment at any age and length. Concurrent increase in the slope of the investment/body length reaction norm (*Length*Year* interaction in Table 1) indicates that investment now occurs at a larger size. The magnitude of these changes was inversely proportional to the age (*Length*Year*Age* interaction in Table 1).

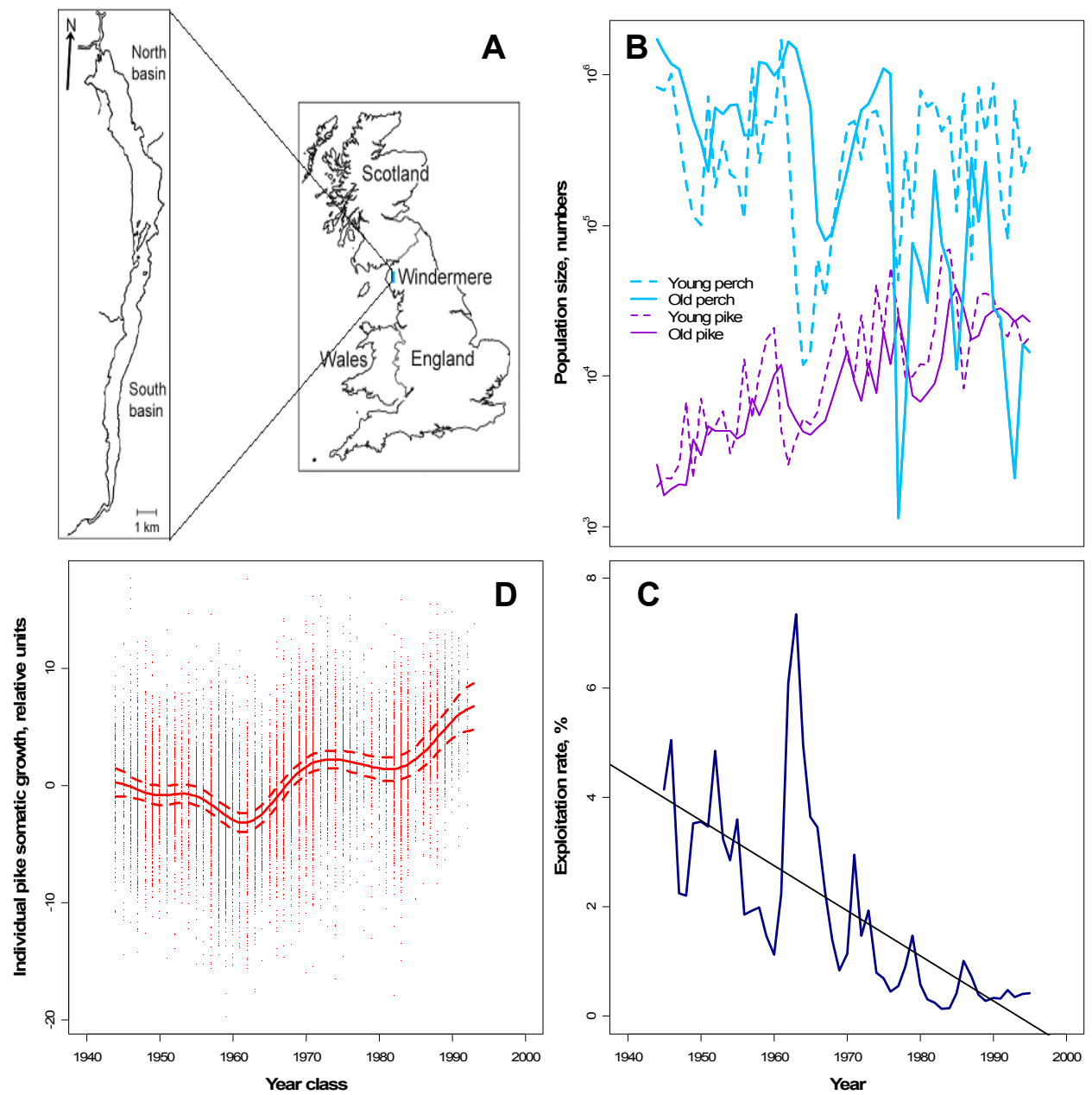


Fig. 1

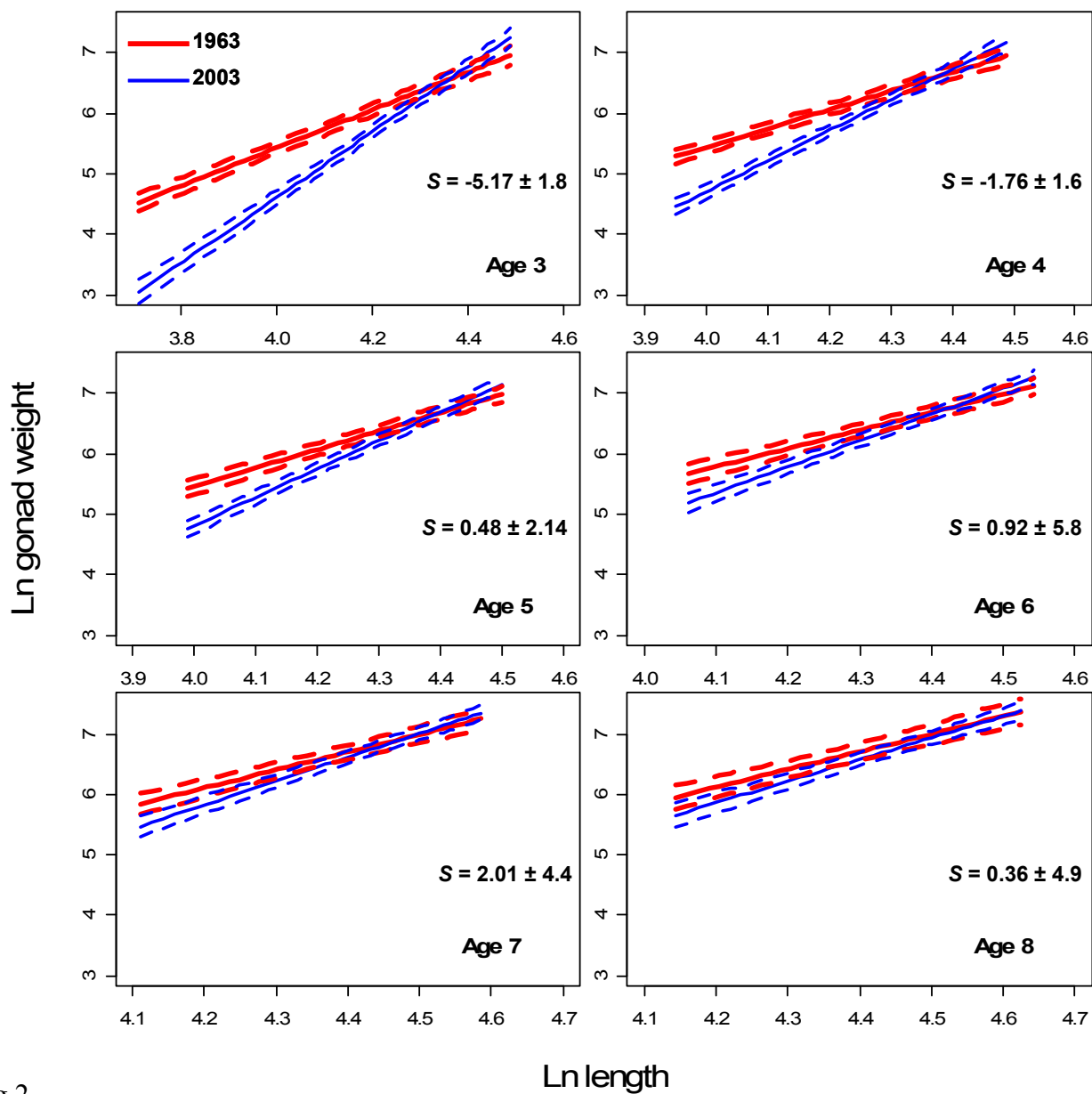


Fig.2

Table 1. Parameter estimates and their statistical significance in the different mixed effects models used to model temporal changes in vital rates of Windermere pike.

Response	Random grouping factor	Fixed effects	Estimate	F-value (numerator df, denominator df)	p-value
Length at age	Individual (13,942 levels)	Temperature (degrees C)	3.80 e-1	2.95 e+3 (1, 51166)	<0.0001
		Young pike (numbers)	1.63 e-4	7.86 e+3 (1, 51166)	<0.0001
		Old pike (numbers)	1.08 e-4	3.14 e+2 (1, 51166)	<0.0001
		Young perch (numbers)	-4.00 e-6	2.60 e+3 (1, 51166)	<0.0001
		Old perch (numbers)	-7.46 e-6	6.55 e+3 (1, 51166)	<0.0001
		Basin (2 levels)	2.87 e-1	1.27 e+2 (1, 51166)	<0.0001
		Sex (females relative to males)	1.19 e+1	3.70 e+4 (1, 51167)	<0.0001
		Year (numbers)	1.58 e-1	1.65 e+5 (1, 51167)	<0.0001
		Temperature*Young pike	-1.33 e-5	1.61 e+3 (1, 51166)	<0.0001
		Temperature*Old pike	-1.60 e-6	7.80 e+3 (1, 51166)	<0.0001
		Temperature*Young perch	4.05 e-7	1.46 e+3 (1, 51166)	<0.0001
		Temperature*Old perch	7.14 e-7	2.12 e+3 (1, 51166)	<0.0001
		Sex*Year	2.01 e-1	2.79 e+3 (1, 51166)	<0.0001
ln Gonad weight	Year (factor variable, 39 levels)	Month	-2.20 e-2	9.38 e+1 (1, 3023)	<0.0001
		Kns (somatic body condition)	6.20 e-3	4.94 e+1 (1, 3023)	<0.0001
		ln Length (cm)	4.01	7.21 e+3 (1, 3027)	<0.0001
		Age (numbers)	-1.55 e-2	6.15 (1, 3027)	0.0132
		Year (numbers)	-6.79 e-3	1.59 e+1 (1, 37)	0.0003
		ln Length*Age	1.59 e+1	2.49 e+1 (1,3023)	<0.0001
		ln Length*Year	8.15 e-2	7.00 e+1 (1, 3023)	<0.0001
		Year*Age	3.46 e-2	1.64 (1, 3023)	0.2004
		ln Length*Year*Age	-8.10 e-3	9.30 (1, 3023)	0.0023
Egg weight	Year (factor variable, 39 levels)	Month	-8.38 e-5	3.74 e+2 (1,3023)	<0.0001
		Kns (somatic body condition)	3.20 e-6	2.20 (1, 3023)	0.1382
		ln Length (cm)	1.43 e-3	2.98 e+1 (1, 3027)	<0.0001
		Age (numbers)	-9.33 e-6	2.88 e-1 (1, 3027)	0.5915
		Year (numbers)	-4.97 e-6	1.29 (1, 37)	0.2627
		ln Length*Age	4.05 e-2	1.95 e-1 (1, 3023)	0.6592
		ln Length*Year	1.57 e-4	2.42 (1, 3023)	0.1196
		Year*Age	8.33 e-5	9.62 (1, 3023)	0.0019
		ln Length*Year*Age	-2.04 e-5	6.96 (1, 3023)	0.0084
ln Egg number	Year (factor variable, 39 levels)	Kns (somatic body condition)	4.96 e-3	4.75 e+1 (1, 3024)	<0.0001
		ln Length (cm)	3.56	3.62 e+3 (1, 3028)	<0.0001
		Age (numbers)	-1.34 e-2	8.80 (1, 3028)	0.0030
		Year (numbers)	-3.32 e-3	8.3 (1, 37)	0.0065
		ln Length*Age	4.14	4.58 e+1 (1, 3024)	<0.0001
		ln Length*Year	2.07 e-2	9.1 (1, 3024)	0.0026
		Year*Age	1.04 e-2	3.8 (1, 3024)	0.0513
		ln Length*Year*Age	-2.17 e-3	1.1 (1, 3024)	0.2965